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Zusammenfassung

Das Interpretieren sozialen Verhaltens von Waldbisons anhand von Schwanzhaltungen

Freilebende Waldbisons wurden beobachtet, um die Schwanzhaltungen während sozialer Interaktionen zu studieren. Unsere Beobachtungen lassen auf die nachstehenden Folgerungen schließen: 1. Unterschiedliche Schwanzhaltungen wurden in unterschiedlichen sozialen Zusammenhängen gezeigt. Schwanzwedeln hing mit Grasen zusammen, während ein waagrecht angehobener und ein aufrechter Schwanz sowohl mit aggressivem und sexuellem Verhalten, als auch mit Gefahr in Zusammenhang gebracht werden konnten. 2. Wenn Kühe und Bullen sich gemeinsam in einer Gruppe aufhielten, zeigten Kühe einen aufrechten Schwanz in Gefahrensituationen und Bullen während sexuellen Verhaltens. 3. Während aggressiver Interaktionen zwischen Bullen hing ein aufrechter Schwanz mit dominantem Verhalten und Schwanzwedeln mit subdominantem Verhalten zusammen. 4. Ein aufrechter Schwanz wurde in extremeren Situationen gezeigt als ein waagrecht angehobener Schwanz. Also war ein waagrecht angehobener Schwanz eine gemäßigte Form von einem aufrechten Schwanz. 5. In Spielkämpfen zeigten Bisons keinen aufrechten Schwanz, während bei ernsthaften Kämpfen zumindest einer der Kämpfenden am Ende des Kampfes einen aufrechten Schwanz zeigte. Das Beobachten von Schwanzhaltungen kann als ein objektives Mittel zur Interpretation des Sozialverhaltens von Bisons dienen. Die mögliche Rolle von Schwanzhaltungen in der Kommunikation von Bisons wird diskutiert.

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Social environment of Isard kids, *Rupicapra pyrenaica p.*, during their ontogeny

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Abstract

Investigated the monthly social environment of cohorts of young isards, *Rupicapra pyrenaica p.* during one and a half years, in an attempt to understand some aspects of their socialization process. We postulate that the sociality of adults is greatly influenced by their ontogeny. The composition, in age-sex classes, of 2,001 groups observed in open mountainous environment is described. During their childhood, young isards go through high sociality periods, during which they are in contact with many and various conspecifics. During other periods, they are in closer association with females only. Both association patterns may play a role in the socialization process. Contact with males is less frequent and occurs for the first time during the rutting period. The most drastic changes in the social environment of the young occur with the arrival of the new generation of kids. The high sociality period of spring is a rather sensitive period during which social associations are very diversified, and social networks may be reshaped. The role of ontogenetic experience in formation of social associations is discussed.

Introduction

The social structure of wild ungulates has been the subject of many studies. Comparisons of data concerning various populations of a given species under different ecological conditions have often indicated intraspecific variations in social systems (LOTT 1983). This suggests that a species do not have a fixed specific social organization or structure, but that both vary greatly under different environmental conditions (HIRTH 1977; SCHAAL 1982; LOTT 1983; ALADOS 1985; MAUBLANC et al. 1987). According to LOTT, this would make developmental questions more salient. BERGER (1979b) noted from reviews describing adult spacing patterns that only few authors considered the process itself, i.e., the ontogeny of social behaviour. He stated that, in Bighorn sheep *Ovis canadensis*, social behaviour and subsequent spatial associations of lambs were influenced by the size of groups within which they were reared (BERGER 1979a, b).

An individual exhibits a social predisposition depending on its sex, age and social experience during its ontogeny, within the limits of specific characteristics (MASON 1978). This social tendency develops in a social and physical context, in constant dialectic interaction with it. Each new generation modifies all existing relations in a group, and receives the influence of the whole group as feedback (BON and CAMPAN 1989). An individual goes through an "ontogenetic trajectory" (MASON 1978; WILEY 1981; BON and CAMPAN 1989), shaped both through internal and external constraints.

This study is based on the assumption that the social context is the framework in which behaviour develops and thus that shapes it into that of the full adult. The sociality of the isard is thus dealt with through a developmental approach. The results are presented in terms of kids' social environment, which is a more "animal centered" approach than a mere description of the social structure in different group types or sizes. Moreover, the information presented may provide the basis for future comparative investigations in isards.

Materials and methods

Observations were made in the National Wildlife Reservation of Orлу, in the Pyrénées Mountains, France. In this area, the isard, *Rupicapra pyrenaica pyrenaica*, a species close to the chamois *Rupicapra rupicapra*, but now considered as distinct (NASCETTI et al. 1985; MASINI and LOVARI 1988) has been protected since 1943. The population reached a high density of about 30 animals/100 ha based on annual counts made by the National Game Agency, responsible for the management of the reservation. Most of the observations were made on about half of the protected area, which covers 4,265 ha. The altitude ranged from 1,400 m in this valley, up to 2,765 m for the highest summit. Vegetation consisted mainly of meadows in the valleys, beech forest with *Fagus sylvatica* up to 2,000 m, some mountain pine forest, *Pinus uncinata*, and alpine pasture above.

Data were collected from May 1989 to December 1990. A "group", at any given time, was distinguished from a neighbouring one when the distance between them was greater than the average inter-individual distance within the group (CLUTTON-BROCK et al. 1982). Under field conditions, this generally corresponded to intergroup distances of 50 m or more (BERDUCOU and BOUSSES 1985; RICHARD and MENAUT 1989; RICHARD and PÉPIN 1990). All visible groups observed on wide panoramas from fixed observation points were recorded throughout the day. Hence, the data only concern observations in open habitats in which visibility was sufficient. Groups were described by their location on an aerial photograph and by the number and nature of their components. 15,179 animals in 2,001 groups of known composition were recorded (9.2% males, 43.3% females, 47.5% young). In this study we generally referred to "mixed groups" as associations containing males, females and young, and to "matriarchal groups" as ones without males.

This work describes the monthly social environments of cohorts of young born in the same year. The field work was conducted over a period of 1.5 years, so the young born in 1988 were observed at the age of 1 to 2.5 years, those born in 1989 from birth up to 1.5 years, and the 1990-generation from birth up to 7 months. Ages were estimated in months as all births were relatively synchronous.

Since the study was centered on the ontogeny of associations of young animals, no strict classification was used to separate them artificially into pre-determined classes. The customary classification of animals as kids, yearlings and subadults did not suit this study, because it created artificial gaps in calculating proportions of various classes at the very sensitive period of parturition. Such artifacts would hide the behavioural events occurring during the same time.

To describe the social environment from the "young's point of view", the young were named with reference to a focal cohort Y. Thus, Y+1 refers to the previous generation (young 1 year older than the focal ones), Y+2 refers to animals 2 years older, Y-1 to the succeeding generation, (1 year younger) and Y-2 to animals two-years younger.

For the sake of clarity, we use "kid" to refer broadly to less than one-year-old young, "yearling" for one- to two-year-old young, and the general term "young" for animals less than 2.5 years old. "Elders" refers to non-adult animals older than the individual in question.

As it is very difficult to determine the ages of adult isards (because of the poorly defined annual horn growth and the large inter-individual variations) individuals of 2.5 years of age or more were simply separated into sex classes: adult female (F) and adult male (M).

The results are presented as percentages of animals of each age class involved in various types of associations. This accurately represents the real distribution of animals in different groups, and thus their social experience, better than the commonly used system enumerating the proportions of groups encountered, which does not take into account group size (BARRETTE 1991). The sizes of different associations are described here by the "Typical Group Size", calculated using JARMAN's (1974) formula:

$$TGS = \frac{\sum_{i=1}^n (G_i)^2}{\sum_{i=1}^n (G_i)}$$

where G_i is the group size of each of the i groups considered. Typical Group Size is also a more animal-centered estimation, representing the group size experienced by the majority of animals, in other words by the "average individual". This value is especially suitable for species that form many small groups and few large ones (HILLMAN 1987), or for species in which groups are very fluid (BARRETTE 1991). Actually, both these conditions were present in our population.

Since our data concern individuals distributed in various group types, the samples are distributed nonuniformly, and are not independent (when several kids are in the same group, they are not independently distributed). Statistical analysis was not attempted in our study for the same reason as that stated by FESTA-BIANCHET (1986) and since sample sizes were sufficient to make the figures for variations of proportion reliable.

Results

Social associations of young up to 1.5 years of age

Monthly variations of the young/female ratio is presented in Figure 1, showing that the period of parturition was very short. The first kids were observed on the 20th of May, 1989 and almost all of them were born by the beginning of June. The ratio kids/females seemed to be rather stable during the first year.

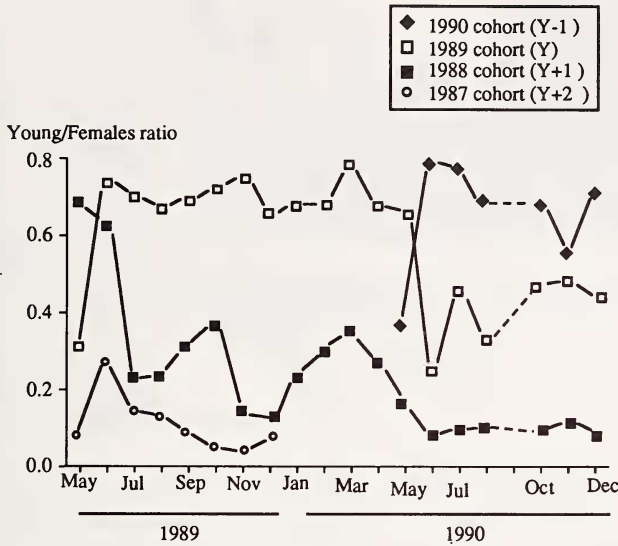


Fig. 1. Young/female ratio for 4 temporary cohorts of young, during 1.5 annual cycles

During their first 7–8 months of life, kids were mostly observed associated with females only, or with females and elders (Fig. 2a). Exclusive association of kids with females decreased during summer, and increased slightly again at the beginning of winter (Fig. 2a, c). Two categories of elders were distinguished for 1990 (Fig. 2c), indicating that kids were in contact earlier with one-year-old animals (June), rather than with the two-year-olds. From May to December, only about 10 % of the kids were not in groups containing peers. These occurrences corresponded to isolated mother-kid dyads, or, to a lesser extent, to mother-kid-yearling trios.

Females were always present in the kids' social environment. Young kids (up to 9 months old) were never observed without the presence of at least one female (Fig. 2b). The presence of kids in mixed groups, with at least one male, increased steadily during the summer and the autumn. This was particularly obvious during the second study-year (Fig. 2c). In November (Fig. 2b), at the peak of the rutting period, the frequency of observations of kids in mixed groups reached its maximum (44 %).

In the winter (January–February) eight-to-nine-month-old kids were involved mainly in complex associations: 48 % with older young (Y+1) and females, 32 % within mixed groups (Fig. 2) and the remaining 20 % were with females only.

The following March, when they were ten months old, more than half of the young were again associated with females only. This increase may be related to the peak of the young/female ratio in March (Fig. 1). Spring was also marked by a second rise of frequentation of mixed groups in April and by the emergence of associations with other young and/or males without any female. It reached its maximum in May (Fig. 2b).

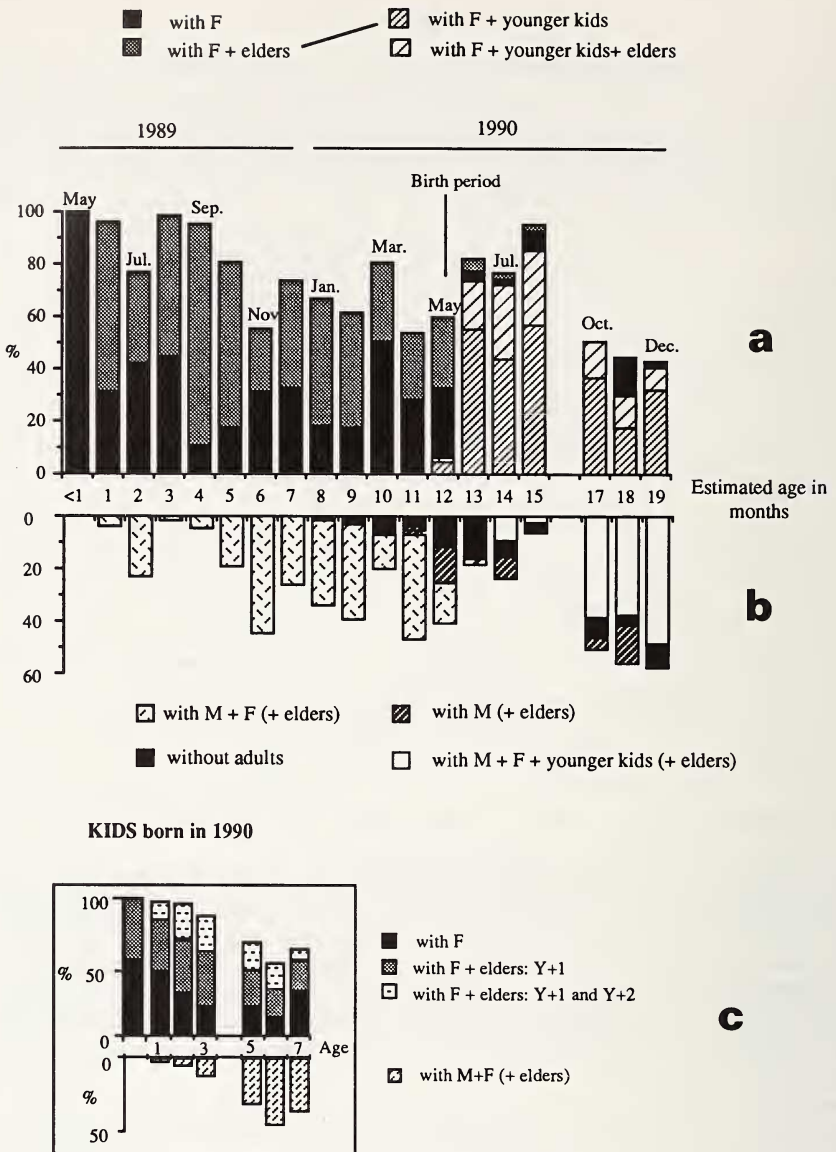


Fig. 2. Patterns of association of young between birth (in 1989) and 1.5 years of age. a: associations without males; b: association with at least one male or without adults; c: young born in 1990

The most noticeable irregularity in these smooth seasonal variations occurred in May, when the mothers left their offspring and isolated themselves to give birth. At that time, the young/female ratio dropped abruptly (Fig. 1). This reflects the sudden break off the exclusive bond between young and mother. During this period, the young presented the largest diversity in their associative tendencies: 14 % with peers and males, 27 % alone with females, 26 % in matriarchial groups and 12 % in mixed groups (Figs. 2, 3). It is of interest to note that, as observed during the first 8 months, about 10 % of the kids were not in contact with peers in groups.

In June 1990, while almost all females had given birth, all the yearlings massively joined females with their newborn kids (Fig. 2a), and also some elders as we already observed in the previous May (1989). Note that before and after birth, these two kinds of groups (young with F, Y+1, Y+2 as well as young with F, Y-1, Y+1) were both composed of females and three generations of young. However, for the focal kids, social environment was quite distinct since, in the first case, they stayed only with elders, whereas in the second case, they were with elders and younger, and had lost the primacy of the bond with the mother.

The young/female ratio increased again in July 1990 (or even later in 1989), but some yearlings probably became dispersed, since this ratio never regained the previous level (Fig. 1). The association of one-year-old young with females and new-born kids (Y-1) was predominant during Summer 1990; only a few stayed apart from the females, and were associated with siblings and males. Although we could not always confirm their sex, we feel the majority of the latter group were young males.

Social associations of young between 1.5 and 2.5 years of age

Figure 3 shows the generation of young born in 1988. One-year-olds (in Summer 1989, Fig. 3a) were more often associated with elders (Y+1) in matriarchial units (52% in

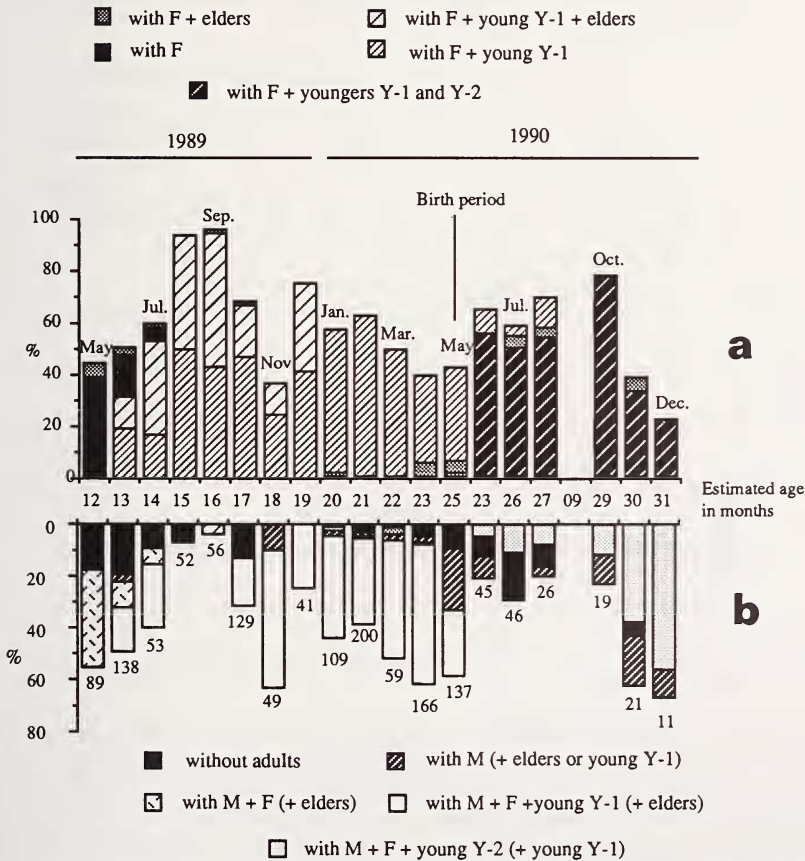


Fig. 3. Patterns of association of young (born in 1988) between 1 and 2.5 years of age. a: association without males; b: association with at least one male or without adults

September 1989) than the one-year-old young observed in the following summer (29% in August 1990, Fig. 2a).

In November 1989, at the peak of the rutting season, 53% of the yearlings were observed in mixed herds, while 36% were in matriarchial ones. They were in reversed proportions compared to the months before and after. In 1990, yearlings born in 1989 were observed in mixed herds from October to December (Fig. 2b).

In the winter, most of the 20-month-old young were still involved in matriarchial or mixed units until the next breeding season, while the 25-month olds once more tended to associate with peers or with males (Fig. 3). Later, they were observed mainly in matriarchial groups, and again joined mixed associations that were formed in November.

Associative tendencies of adult females

As grouping with females is very important in the social environment of the kids, it is of interest to note that association of females with males occurred mainly between October and April (Fig. 4). These mixed associations, with several generations of young, corresponded, most of the time, to large gatherings in favourable grazing areas. These were the largest type of association and reached a maximum in April and in November 1990 (Table 1). During the summer, the sexes were separated, (with a brief exception in July 1989), and most of the females were observed in matriarchial groups. About 15% became isolated or formed small all-female units in the breeding period (May).

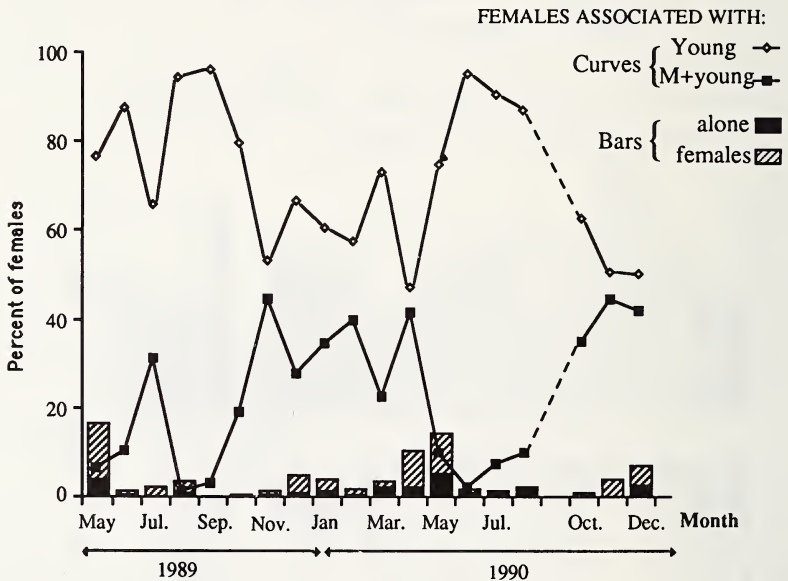


Fig. 4. Patterns of association of adult females during 1.5 annual cycles

The frequency of female associations with kids only decreased from parturition and during the rearing period, but reached a new peak in March. During the summer, females with newborn kids progressively frequented groups of increasing social complexity.

Typical Group Size of female-kid groups reached its maximum just after parturition (Tab. 1): about 15 in May 1989, and 27–33 in May–June 1990. It then sharply decreased during the summer (about 4 in August or September).

Matriarchial associations (containing at least 2 generations of young: FY), were largest

Table 1. Typical Group Size (TGS) and mean group size (mgs) of the various associations

	Year 1989												Year 1990											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.				
ALL	TGS	42	26	18	22	32	23	43	65	40	40	54	79	48	33	25	28	-	24	36	8			
	mgs	7	7	8	7	16	10	13	13	13	12	11	20	12	11	9	10	-	10	14	4			
MFY	TGS	20	28	28	-	18	22	44	19	29	55	24	94	72	19	30	19	-	41	55	12			
	mgs	31	21	20	-	52	16	32	13	19	28	19	61	40	17	16	18	-	34	34	10			
MM	TGS	16	2	-	2	-	5	3	2	2	3	7	10	10	7	12	-	-	6	5	2			
	mgs	8	2	-	2	-	4	3	2	2	3	6	7	6	8	6	-	-	3	4	2			
MY	TGS	13	5	-	-	-	-	2	2	2	8	2	16	16	7	23	3	-	11	16	4			
	mgs	10	5	-	-	-	-	3	2	2	6	2	13	12	6	12	3	-	8	10	4			
YY	TGS	6	5	3	2	-	3	-	1	3	5	3	2	4	3	2	1	-	2	1	2			
	mgs	6	3	3	2	-	3	-	1	2	4	2	2	3	2	2	1	-	2	1	2			
FK	TGS	15	7	7	6	4	5	9	8	10	9	7	6	27	33	8	4	-	5	6	3			
	mgs	14	4	5	5	3	4	6	5	5	5	5	4	15	8	5	3	-	4	4	3			
FY	TGS	7	41	12	25	24	17	22	24	27	20	10	12	30	30	18	18	-	13	16	9			
	mgs	7	13	9	11	16	11	12	13	15	13	9	10	16	16	12	13	-	8	13	6			

ALL = groups with all categories of individuals; MFY = groups including male(s), female(s) and young; MM = male groups; MY = groups including male(s) and young; YY = groups of young; FK = female(s)-kid(s) groups; FY = females with at least 2 generations of young.

in June 1989 (TGS = 40), and in May-June 1990 (TGS = 30; Tab. 1). During Summer 1989, although the most of the kids, yearlings and females were in this type of herd, these groups were scattered in small units.

Associative tendencies of adult males

As males were part of the social environment of kids and young at least at some periods of the year, it is of interest to look at the associative tendencies of the males themselves. During the year, on average, about 33 % of the adult males grouped together and up to 87 % if we consider that the male-young associations observed in May concern mainly young males. The relative proportion of these all-male associations reached its minimum in winter (16 % in December 1989 and in November 1990). Around 10-30% of the males were observed alone, others in mixed associations with females and young, mostly during Winter 1989 and Autumn 1990.

The size of male-male associations reached its highest peak in April-May, as did male-young and young associations. However, this type of group was not more frequent at this period, only the number of animals per group was higher (up to 22 adult males).

Discussion

Following the social environment of the kids of *Rupicapra pyrenaica*, one can project the presence of a pattern similar to that proposed by BON and CAMPAN (1989) for moufflons, and trace a "standard ontogenetic social trajectory" of an "average individual". Each step of such a trajectory as well as the variations of the social environment along the yearly life cycle, may be influenced by either biological or ecological factors.

Isolation for parturition is a well known phenomenon, described in most ungulate species, wild or domestic (LENT 1974). It allows the establishment of an exclusive bond between mother and newborn, each learning to recognize the other individual (LENT 1974; LICKLITER and HERON 1984; POINDRON et al. 1984). Mother-kid association is generally considered to be the basis of ungulate sociality, and often as the only stable entity (BOUISSOU and HÖVELS 1976; GONZALEZ and BERDUCOU 1985; BON et al. 1986). In "follower" species, kids stay close to the mother during their first weeks of life, and accordingly are found together within the same groups (EPSMARK 1971; LENT 1974). Social environments of kids initially seem to depend mainly on those of their mothers.

After parturition, in our population of isard, mothers gather together in large flocks (up to 40 females) in open areas, each one followed by her kid. The kid/female ratio is usually 1 in such groups. FERRARI et al. (1988) related these matriarchial groupings in the Appenine chamois *Rupicapra pyrenaica ornata* to the particular diet of females during lactation and early weaning of kids. On the other hand, HILLMAN (1987) thought that, in the common eland *Tragelaphus oryx* aggregations of females with young might be due to the active gathering of the calves, which were physically attracted to one another. In this case, the females follow their offspring into those gatherings. In our study, although kids seem to follow primarily their mothers, they also have a great attraction for peers, which might play a role in the formation of the post-breeding nursery groups. These associations were actually the first occasion of high social interactions in the kids' experience, and the kids often strayed away from their mothers and had many contacts with peers and engaged in long sequences of play involving most of them (RICHARD-HANSEN 1992b). Additional yearlings joined these associations, staying more or less peripheral, and providing new social partners for the kids and a progressive enrichment of the social context. These large flocks seemed to include, for a short time, most of the females, who usually and independently frequented partly overlapping home ranges, as demonstrated by following some marked animals (RICHARD-HANSEN, unpubl. data). However, differences may exist in the social environment of the kids. In the Ossau population (another area of the Pyrénées) BERDUCOU and BOUSSES (1985) observed 1/5 of isard kids in mixed herds as early as June.

In our observations, the large nursery flock did not last more than 1–2 weeks (end of May–beginning of June) after which most of the animals moved up to summer ranges. We suspect that they moved to the higher altitudes to find more rocky areas, to avoid heat, direct sunshine or insect harassment, as well as pressure from domestic animals that range on alpine meadows.

In the summer home ranges, the groups were smaller during mid-day and in many instances were reduced to mother-kid or mother-kid-yearling units, the animals spending these hot hours lying down in narrow shaded shelters, behind rocks (PÉPIN et al. 1991). Larger herds of isards occurred in the morning and in the evening, when the small units, hardly observable during the day, gathered to graze on prairies (PÉPIN et al. 1991). Males were seen to join these flocks for short periods, especially in the highly attractive zones, where salt-licks were laid out for domestic sheep and cows (HANSEN et al. 1992; INGOLD and MARBACHER 1991). Similar observations of smaller group sizes of moufflons in the summer were made by BON and CAMPAN (1989). These authors proposed that the small group sizes were formed in response to high temperatures and impoverishment of the

meadows. It is of interest to note, however, that other studies on the chamois (ELSNER-SCHACK 1985; KRÄMER 1969) or Appenine chamois (LOVARI and COSENTINO 1986) have shown the opposite to be true, maximum group size being attained in summer.

Isards came back to their previous home range during September, which seemed to be a transitory period. Latter on, during the rutting period, many kids were included in large flocks gathered on prairies. Males, actively looking for mates, were then running from one group to the other and temporarily becoming part of them. Once more, we may note differences between distinct areas: while 80 % of the females belonged to mixed associations in Ossau in November (BERDUCOU and BOUSSES 1985), less than 50 % did in Orlu. This difference can be related to the higher proportion of mixed groups in the Ossau population. Thus, in our study as in the Carlit population (a further area of the Pyrénées, GONZALEZ and BERDUCOU 1985), kids were in sustained contact with males for the first time in their lives in November, i.e. during the rutting season. BON and CAMPAN (1989) also noted that 7–8 months-old moufflon lambs *Ovis ammon musimon* joined mixed groups, following their mothers, in the rutting season. During winter, the animals were usually found at higher altitudes (about 2,000 m) where cliffs, high slopes and windy ridges reduce the thickness of snow. Thus it appears that the causes of this move, like that in summer, are mainly environmental factors. Actually, when there was no snow, as occurred during the Winter of 1989–1990, most animals continued to frequent the pastures.

In March, as they approached one year of age, the young went through a period of reinforcement of exclusive association with females, as shown by the increase in the percentage of this type of association, and of the young/female ratio. We already suggested in a previous study (RICHARD and PÉPIN 1990) that kids could go through regressive periods in their development, during which they stayed closer to females and spatially more central within the groups, as observed for 1–2 month-old kids. This may have important implications in the social system by its possible causal value explaining the formation of matriarchial associations of females and daughters as suggested by HORWITCH (1977) for the ibex. This hypothesis still has to be confirmed by estimation of mother-kid distances and kid's behaviour. LOVARI (pers. comm.) also suggested that Appenine chamois in Abruzzo *Rupicapra pyrenaica ornata* may form matriarchial units in which daughters stay with their mothers. Furthermore, one marked mother-daughter dyad in our study area remained closely associated for over two years (RICHARD-HANSEN 1992a), until they were broken up by accidental death.

April was another period of high sociality with formation of very large herds on the lower prairies, where the grass grows first. These aggregations, certainly due to feeding opportunities, were also the occasion of intense social contact between yearlings, gathering into subgroups of peers, leading to the groups of young observed in April and May. Some males were also present in these gatherings, integrated or in separate male groups, and some yearlings were observed to follow them very closely and appeared to be integrated into the groups, as shown by emergence of "MY" associations. In the Ammergau Mountains, Bavaria (ELSNER-SCHACK 1985), seasonal factors had inverse consequences: in this area, smallest group sizes were observed in spring and autumn, due to scattered food sources.

During the parturition period, in May, we observed many associations of young, as more and more females isolated themselves. Most authors state that these juvenile associations exist during parturition or during summer, in various ungulate species: isard (GONZALEZ and BERDUCOU 1984; BERDUCOU and BOUSSES 1985), Spanish ibex (ALADOS 1985), white-tailed deer (HIRTH 1977), Siberian ibex (HORWITCH et al. 1977), moufflon (GONZALEZ and BERDUCOU 1985; BON and CAMPAN 1989), reindeer (EPSMARK 1971), and red deer (CLUTTON-BROCK et al. 1982). The wide variety of social environments of young described in this study at this transitory period of parturition reflects the instability of their

Table 2. Overall view of social and physical environments experienced by kids during their ontogeny

Period	Age in months	Biological event	Type of association	Physical environment
May	0	Birth	Mother-kid dyad	Parturition area
June	1	Early rearing	Large mother-kid flocks	Alpine pasture
July	2	Waning	smaller scattered matriarchal groups few contacts with males	Hot weather domestic flocks High altitude, summer home ranges rocks, shadow large pasture
August	3			
September	4			
October	5	Rut	mixed flocks	
November	6			
December	7			
January	8		Median size mixed or matriarchal herds	Snow high altitude rocky cliffs and ridges
February	9			
March	10		Females-kids groups	
April	11		Large mixed flocks	Lower pasture with spring grass
May	12	Mother's isolation	Diversity of grouping	
June	13		Juvenile associations	
July	14		Yearling females join nurseries	Alpine pasture
August	15		Some yearling males join male groups	Former summer home ranges
September	16			
October	17	Rut	Mixed flocks	Former pasture
November	18		Yearling females participate in rutting associations	
December	18			
January	20		Mother-yearling daughter associations	Snow high altitude rocky cliffs and ridges
February	21		with or without males	
March	22		Large mixed flocks	
April	23		Some yearling females became isolated	
May	24	Possible parturition	Associations of young	Lower pasture with spring grass
June	25		Matriarchal associations with young	Former summer home ranges
July	26			
August	27			
September	28			
October	29			
November	30	Rut	Mixed flocks	Former pasture
December	31			

status, as well as their great plasticity of grouping behaviour. Most of them rejoined nurseries of females with newborn kids during the summer. In June, half the yearling isards were observed in female-young groups in Ossau (BERDUCOU and BOUSSES 1985), whilst 4/5 were observed in Orлу at the same time. This difference, as noted before for kids, can be related to the higher proportion of mixed groups in the Ossau population. It is possible that some of the yearlings may disperse, or follow adult males, as the young/female ratio did not recover the pre-parturition levels. CLUTTON-BROCK et al. (1982) also reported, in red deer, a marked decline of mother-calf association during the new calving period, followed by an increase during the summer, which never reached the same level as that observed previously.

Young isard females are sexually mature and may already participate in reproduction in the second autumn of their life, as proved by a marked 2-year-old female observed nursing a kid in July. Table 2 shows a general view of the whole standard social trajectory with the various factors that might shape it.

On the one hand, social environment and, consequently, the social ontogenetic trajectory of an individual isard is, all along its path, submitted to external constraints. In our work as in many other studies, weather and snow-cover conditions were shown to have a great influence on the distribution of food and on the animal's pattern of habitat use (PETOCZ 1972; HIRTH 1977; LAGORY 1986; BON et al. 1990). In this work as in others, the presence of very large prairies, for instance, proved to be responsible for large gatherings (CLUTTON-BROCK et al. 1982; SCHAAL 1982; MAUBLANC et al. 1987). But all the external constraints that can occur are different, for a given species, amongst the various living areas, and even within the same area, between various home ranges. Furthermore, these environmental conditions are not similar from one year to another. Thus, the social environment of an individual isard appears to be fluid, and its own social experience is distinct from that of its conspecifics.

On the other hand, it is clear that biological events play a major role in shaping the individual social trajectories through various social environments. They are: a. experience before birth, through maternal stress for instance (LOTT 1983), b. early mother imprinting (LENT 1974; BOUSSOU and ANDRIEU 1978; BERGER 1979a; LICKLITER and HERON 1984; POINDRON et al. 1984), c. mating (MIURA 1983), d. breeding (BON et al. 1990), e. rearing young (FERRARI et al. 1988; HILLMAN 1987). The social context also shapes the trajectory through the relative proportion, density and social trajectories of the conspecifics (BERGER 1979b; CLUTTON-BROCK et al. 1982; ALADOS 1985). These factors act together to bring about a diversity of social environments that each individual will experience, that makes its actual social trajectory unique. The social structures are the complex pictures observed and they result from the network of interacting individuals, themselves influenced by the interacting factors mentioned. Social structures become constructed in the same way as the individuals during their ontogeny. Studying the interactions between individuals should contribute to a fuller understanding of the establishment of such a network, and the self-organisation mechanisms of animal associations (RICHARD-HANSEN 1992b).

On another hand, only long-term studies on marked animals, like the one in progress in the Orлу population, will allow the general rules of the mechanisms underlying the self-construction of a social trajectory to be established.

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